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THE ECOLOGY OF THE WESTERN SPOTTED FROG, *RANA PRETIOSA PRETIOSA* BAIRD AND GIRARD. A LIFE HISTORY STUDY

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Introduction

Numerous individuals have assisted in the preparation and completion of this study. We are indebted to Mr. Lawson Hamblin for allowing free access to his property where the main portion of this study was conducted, and to Dr. Frederick B. Turner for his suggestions and review of the manuscript.

We also thank Mr. David F. Avery for his help and for the data he furnished for the years 1962 and 1963, and also for photographs taken by him. Thanks also to the other students and staff who have helped in data analysis.

Since the turn of the century, the study of amphibian life history has received more attention than before; however, the natural history of many amphibians is still only partially known. Much of our knowledge is based upon laboratory studies where observations have been made on eggs obtained directly from the female as described by Rugh (1948) and as used by Johnson (1965), or directly from the pond as reported by Skousen (1952, unpublished). These types of studies provide for controlled conditions thereby giving a low variance to the results. They can also give an actual growth curve rather than an estimated one since the same individuals can be studied continually throughout their larval development. However, as stated by Bragg (1940a), to understand the reactions and behavior of an animal within its complex environment, one must still of necessity go directly to nature. Therefore, this study is based on an empirical approach.

Review of Literature. Since the description of *Rana pretiosa* Baird and Girard, only limited life history accounts have appeared

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in the literature as compared to most other species of this genus in North America. Most references are small notes relating to distribution, habitat, or stomach content, and refer to populations occurring in Oregon, Washington, British Columbia, Wyoming, Idaho, and Utah. A brief summary is given by Stebbins (1951 and 1954).

Several accounts of *R. pretiosa* have appeared since the reports by Stebbins. Turner (1957) did a four year study from 1953-1956 on the ecology and morphology of *Rana pretiosa pretiosa* at Yellowstone Park in Wyoming, and Johnson (1965, unpublished) worked on the early development, embryonic temperature tolerance, and rate of development of *Rana pretiosa luteiventris* Thompson, from central Oregon. *Rana pretiosa* has also been included by Dunlap (1955) and Dumas (1966) in excellent works on the genus *Rana*. The influence of nerves in limb regeneration was studied by Thornton (1956) on *pretiosa* tadpoles taken at Moran, Wyoming.

Other earlier papers include Svihla's (1935) brief report on the eggs and tadpoles of *pretiosa* in Washington; Middendorf's (1957) observations on the frog's early spring activities in Montana; Carpenter's (1953a) brief ecological notes on *pretiosa* in the Grand Teton-Jackson Hole area of Wyoming, and his (1953b) notes on the aggregation behavior of the tadpoles. In a later study on amphibian movement, Carpenter (1954) found that there is a tendency for individuals to return to their original point of capture. Dunlap (1959) described briefly some morphological characteristics of *pretiosa* found in Deschutes County, Oregon.

The first published report of amphibians in Utah was by Yarrow (1875); however, no comprehensive work was done on the populations of Utah *Rana pretiosa* until Tanner (1931) included them in his work entitled, "A Synoptical Study of Utah Amphibia." The only other reports to include this species are those of Van Denburgh and Slevin (1915), Slevin (1928) who provides a description, and Skousen (1952) in which he characterized the eggs and larvae of Utah amphibians.

Taxonomic Status

Rana pretiosa was first described from Puget Sound, Washington, in 1853 by Baird and Girard. *Rana pretiosa luteiventris* was later described by Thompson (1913) from Anne Creek, Elko County, Nevada. Although *R. pretiosa* has been recognized as a valid species since its description, the status of the subspecies *luteiventris* has been questioned by several writers. Slevin (1928), for example, did not separate *R. p. luteiventris* from *R. p. pretiosa*. He based this decision upon the work of Van Denburgh and Slevin (1915) which stated that it was not possible to find constant differences in plantar or palmar tubercles between those specimens thought to be *R. p. luteiventris* from Utah and those *R. p. pretiosa* from Fort Klamath, Oregon, and Mount Rainer, Washington. Storer (1925) also questioned the validity of the subspecies *luteiventris* as did Stebbins (1951) when he stated, "it appears to be no more than a slightly differentiated sub-

species of possibly very local occurrence." He did, however, recognize the subspecies *luteiventris* at this time. In a later work Stebbins (1954) did not recognize *luteiventris*, and in his latest work (1966) makes no mention of it.

Dunlap (1955) did recognize the two subspecies in his work on the variation within the genus *Rana* and states:

> *R. p. luteiventris* may be distinguished from *R. p. pretiosa* by the difference in coloration and by the foot tubercles. The bright color on the ventral surface is orange-yellow in adult *R. p. luteiventris*, and bright salmon-red in adult *R. p. pretiosa*. *R. p. luteiventris*, furthermore, lacks the tubercle at the base of the fourth toe, which is characteristic of *R. p. pretiosa*.

Dumas (1966) in his study on the Rana species complex also recognized the validity of the two subspecies. Livezey and Wright (1947) in their work on salientian eggs said that the eggs are entirely different between the two subspecies.

In Utah the subspecies has been recognized as *R. p. pretiosa* by most writers (V. M. Tanner 1927, Stejneger and Barbour 1943, W. W. Tanner 1940, Stebbins 1951, Schmidt 1953); however, certain variations have made its identification confusing. Skousen (1952) stated that the larvae of *R. p.* subsp. of Utah do not fit the description of *R. p. pretiosa* by Svihla (1935), but rather the description of *R. p. luteiventris* by Thompson (1913) and Svihla (1935). He also stated that the eggs are smaller than those of *R. p. pretiosa* of eastern Washington, and, therefore, suggested that the Utah population along the Wasatch front be called *R. p. luteiventris*. In a recent work Dumas (1966) summarized the distribution of *R. pretiosa* subspecies as follows:

> *Pretiosa* (sic) is found from northern British Columbia and southwestern Alberta southward through northern Idaho, western Montana, Washington, northern and western Oregon, and extreme northern California. *Luteiventris* (sic) occurs in southern Oregon, southern Idaho, western Wyoming, and in isolated pockets in northern Utah and northern Nevada.

Much of the confusion over the Utah subspecies is well founded and the decision one reaches in classification is largely determined by the stage of the life history which is studied. We have experienced similar difficulties in an attempt to classify Utah *pretiosa* by the diagnostic features given in the different taxonomic references. Livezey and Wright (1947) published a classification of anuran eggs of the United States and differentiated the *pretiosa* subspecies mainly upon: (1) the number of gelatinous envelopes surrounding each egg, and (2) the size of the eggs and number of the eggs per clutch. When special care is used in the observation of the jelly layers, Utah *pretiosa* key out to subspecies *pretiosa* because of their size and presence of the inner membrane. The differentiation of larvae is based upon the number and size of labial teeth rows. Tadpoles in this case, as pointed out by Skousen (1952), have two upper rows of teeth and fit the description of *luteiventris* by Thompson (1913) rather than

that of *pretiosa* by Svihla (1935). The diagnostic characteristics used in the separation of adults are based upon coloration and the presence or absence of tubercles on the inner surface of the feet. The ventral coloration of live specimens range from orange to red which would place them as *pretiosa*, whereas tubercles are reduced and indistinct which is characteristic of *luteiventris*. Based upon the above information and the fact that some authors question the validity of *luteiventris*, we consider the Utah population to be *R. p. pretiosa* with a few aberrant characteristics which, as pointed out by Skousen (1952), may be the result of intergradation between the two subspecies. This possibility exists since both subspecies are present in the northern regions of the Great Basin and are approximately equal distances from the Utah population. In either case more work is needed on the taxonomy of the species, and the lines of distribution need to be established.

Life History and Ecology

Amphibians are used extensively in different experimental fields of biology and many times this is done without an understanding of the activities and life history of these animals in nature. This lack of information may also have a bearing upon other studies and their results. For example, Johnson (1965) studied temperature tolerance and developmental rate of *R. p. luteiventris* in the laboratory, but was unable to relate these to its distributional pattern based upon the breeding biology because of lack of information on *R. p. pretiosa* and other western species of ranids. In this study we are concerned with life history and breeding biology of *Rana pretiosa pretiosa* in Utah.

Study involves data which have been collected intermittently from 1962 to the spring of 1968 with the majority of the data collected regularly during spring and summer of 1966. This was done by following the activities of frogs from the time they emerged in the spring until offspring metamorphosed and hibernated in the fall. Observations and collections were made at regular intervals throughout this period of activity to provide a continuous record of growth and activity.

The study actually began in the spring of 1962 as a research project by David Avery, but was discontinued when eggs under observation were destroyed by children. The same study was resumed in 1963 except that all observations and measurements were obtained from eggs which were removed from the pond and taken to the laboratory where embryonic and larval development were observed in a 44 liter aquarium until metamorphosis was completed.

To gain a more complete picture of the life history of the western spotted frog, we obtained permission to study the frogs inhabiting the ponds on the private property of Mr. Lawson Hamblin (study area II) during 1966. This proved to be an ideal site, not only because of protected surroundings, but also because *R. p. pretiosa* is the only frog to use these ponds for breeding. As a result no difficulty was encountered in keeping separate the eggs and tadpoles from

those of *R. pipiens brachycephala* which normally occupies the same waters in this area.

Extensive observations were made and specimens collected at these ponds during the spring and summer of 1966. This study is supported primarily by these data, supplemented by additional observations made by us and others both before and after 1966.

Study Areas

Observations on the western spotted frog were made primarily in the vicinity of Provo, Utah, along drainage areas of the Provo River at an elevation of approximately 4550 feet. A population of *R. pretiosa* along the San Pitch River three miles north of Fairview, Sanpete County, and one near Mona Reservoir in Juab County (collection records of adults only) are also included. The area used for this study is at the extreme southeastern extension of the range for *R. pretiosa* (See Stebbins, 1966) and includes those populations which have extended south from Snake River Basin in Idaho into the water courses along eastern edge of the Great Basin and the western front of the Wasatch mountains.

All study area were located after much field investigation, and can be characterized by several features which they have in common. Each site at which *R. pretiosa* has been observed was located, in relation to the local topography, in a low, swampy situation with some type of spring water supply nearby. Except for study area IV all sites were near the base of Provo Bench where water collects as a result of its relative position to the water table. Each observed site is a small permanent pond of water which has a continual source of water. Because of their low level and seep springs inflow, the ponds seldom have an external outlet; therefore, very little movement results because of flow of water through them. As a result each pond is made up of standing water with a deep silt or muck bottom in which frogs presumably hibernate during the winter.

Stonewort, *Chara sp.*, makes up the dominate aquatic vegetation and forms a complete mat covering over the bottom of the pond. Cattails, *Typha sp.*, are present in the deeper parts of each pond, and provide a cool, moist place for adult frogs to feed during the warmer summer months. By the end of June *Spirogyra sp.* is usually common in water providing an excellent place for hiding and a source of food for developing tadpoles, which can normally be found within or beneath floating vegetation.

Study area I was located near the old Provo Brick and Tile Company in a swampy area resulting from several small springs and seepage from higher irrigated lands. The three ponds used as breeding sites were all small ponds of standing water with seepage as the only inlet (Fig. 1). Several other ponds which were interconnected by small streams were present, but none of these were used by the frogs. Study area I has since been filled as a result of construction.

Fig. 1. Main breeding pond at study area I. Arrow indicates location of egg deposition.

Study area II is located at 2160 N. 750 W., 1 mile northwest of area I on property of Mr. Lawson Hamblin. This site consists of four man-made ponds, only two of which were used as breeding ponds. Pond A (Fig. 2) is the only one continually spring fed and therefore has a temperature several degrees lower than other ponds in this specific area.

Pond A measures approximately 5 by 8 meters, and has the smallest surface area. However, it is the deepest pond used for breeding at this location. The depth of the water at the north end is approximately 30 cm. and has a rocky bottom. The south end of the pond, where most of the adult frogs are concentrated, is approximately one meter deep and has a muck bottom. A thick growth of cattails

Fig. 2. Pond A at study area II. Arrow indicates location of egg deposition.

is present at this end. All the ponds are at the base of a 16 to 20 meter embankment (lake terrace) which extends along the west side. Willows growing thickly along the bank hang over the water for approximately one meter. A field with several species of grasses and weeds borders the ponds from the east. Pond B is located 30 meters north of pond A and is much larger, measuring approximately 12 by 21 meters. *Chara sp.* completely covers the bottom of the pond with only a thin layer of water appearing above it. The water is 15 to 45 cm deep with a muck bottom 60 to 90 cm deep.

Study area III is a drainage area from higher irrigated lands and is located west of Provo along the D. & R.G.W. Railroad tracks at approximately 1000 N. and 2100 W. (Fig. 3).

Study area IV (Fig. 4) is the highest elevation 5350 ft., at which observations were made in the Provo River drainage area. It is located on the south fork of Provo River approximately one and one-half miles east of Vivian Park, Utah County. These are permanent spring-fed ponds which have been impounded by man for a water storage area.

Several observations were made on a population of *Rana pretiosa* along the San Pitch River in Sanpete County. This population as reported by Tanner (1940) is the farthest south that this species has been collected. The elevation is approximately 6140 feet and because of the cooler temperature, eggs are laid about two weeks later than they are near Provo.

All ponds exhibit a basic reaction as shown by the pH readings in Table 1.

Fig. 3. Habitat of study area III. Arrow indicates location of breeding activities.

Fig. 4. Hatitat of study area IV.

Table 1. The pH readings taken from study areas.

Location	pH Reading
Study area I	7.45
Study area II pond A	7.50
Study area II pond B	8.48
Study area III	8.52
Study area IV	8.42

Methods and Procedures

Intensive field work has been carried out for the past three years beginning in the early spring months during 1965 to 1967 for the purpose of locating suitable habitats and noting the first dates of emergence. Temperature data taken from the ponds were later compared with temperature data obtained from United States Department of Commerce Weather Bureau Climatogical Data Reports for Provo and Geneva, Utah, to determine the physical conditions of the environment which released frogs from their hibernacula.

Daily observations were made on the breeding and egg laying habits after their spring appearance. Photographs were taken of eggs and mating frogs, and recordings made of breeding call of males in the field with a model 301 Martel Tape Recorder.

All egg clutches were measured in the field and left in their natural surroundings. Clutch dimensions were measured to the nearest centimeter by means of a metric ruler. Volume was determined by water displacement in a 500 ml graduated cylinder. Several eggs were taken from each clutch, preserved in 10 percent formalin, and removed to the laboratory where each egg was examined and measured individually to the nearest 0.1 mm with a 10 power magnification of a dissecting microscope equipped with an ocular micrometer.

To facilitate viewing of the inner membrane of the eggs, several techniques were employed. One such method, useful in the field, was to float a few eggs over the surface of the water in a small, white enamel pan, and then to observe the shadow cast by each membrane on the bottom of the pan when placed in direct sunlight. Although this method was successful for fresh eggs, it was not satisfactory for preserved eggs because of irregular shadows resulting from distortions in the outer surface. Another technique which proved very useful was staining. This was accomplished by first embedding individual eggs in dental impressive material, Hydrocolloid Algenate, according to directions on the label. After approximately four minutes the capsule was cut with a razor blade as close to the center of egg as possible. A drop of either Congo Red or Giesman stain was then placed over the exposed surface for one or two minutes and then removed. The resulting ring or rings within the jelly could then be observed and measured under a dissecting microscope.

Tadpoles were collected randomly at regular intervals and preserved in 10 percent formalin, and all measurements were taken

to the nearest 0.1 mm as follows: head-body length, from tip of snout to the midpoint of cloacal opening; tail length, from midpoint of cloacal opening to tip of the tail. Total length was derived from the sum of the body and tail lengths; widths were taken at widest part of the body. Weights were taken on a Mettler electric balance and read to the nearest 0.1 mg and estimated to the nearest 0.01 mg; tadpoles were placed on blotter paper for 15 seconds after removal from the formalin before weighing.

Egg numbers were obtained by three different methods: (1) by counting eggs in each clutch after ovulation, (2) by counting the number of eggs in a given volume and then measuring the volume of the whole clutch, and (3) by actual count of eggs dissected out of mature females collected at intervals during late summer of 1966 and early spring of 1967.

Some difficulty was encountered during 1965 in locating tadpoles because of the dense growth of vegetation. To facilitate their collection, a small mesh wire screen was placed around the eggs at study area II on March 26, 1966 (Fig. 4 and 5). The screen was approximately 8 meters long and made a semi-circle in the water. The open end of the screen was approximately 3 meters long. The water level at pond A increased progressively during the summer so that it provided no barrier late in the summer. The effect of the screen at pond B is discussed in conjunction with larval development.

Analysis of dissolved minerals in water taken from the ponds was obtained through a measurement of conductivity with a salt bridge. Results are expressed in parts per million.

Hydrogen-ion concentrations were determined with an electric pH meter in the laboratory.

Discussion

The first appearance. The western spotted frog emerges from hibernation normally during the middle of March when the air temperature has risen to 13-16° C for several days or after a rain storm which has warmed the water sufficiently (Fig. 5-8). Spotted frogs appear about one week after the chorus frog *Pseudacris nigrita triseriata* which has been the first anuran to appear in the spring within the time covered by this study. The emergence of the leopard frog *R. pipiens* normally follows *R. pretiosa* by 7-10 days so that by the end of March the chorus frog and both ranids are present in the ponds often in large number. The peaks of the spawning seasons for these species, however, normally do not overlap in a given habitat at the same general elevation.

During the course of this study, earliest record of appearance for *R. pretiosa* was March 6, 1967. The seasonal temperature was unusually warm during this time. More important, however, than the air temperature itself is the temperature of the water under which the frogs hibernate. A temperature of 10-11° C seems to be a critical point in their activity. Not only must the water reach this tempera-

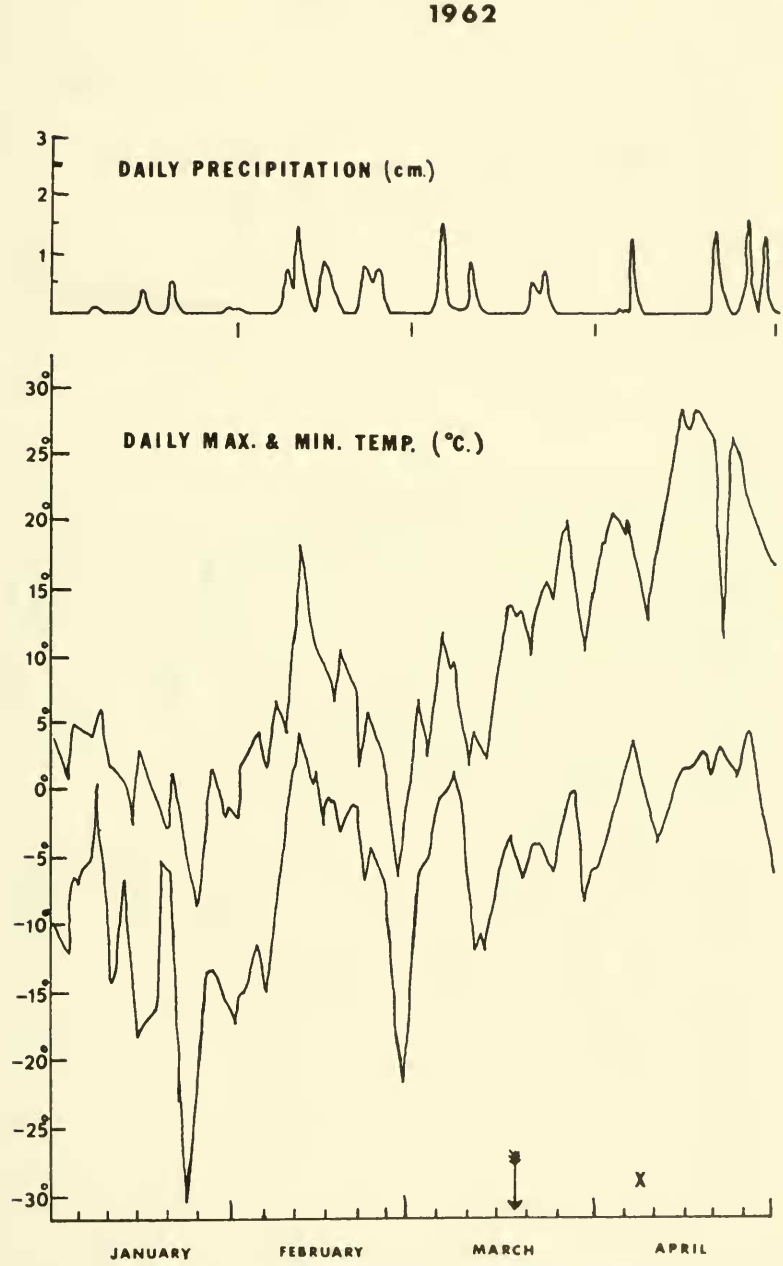

Fig. 5. Climatic data for the spring of 1962. Arrow indicates approximate date of emergence; X indicates approximate date hatching began.

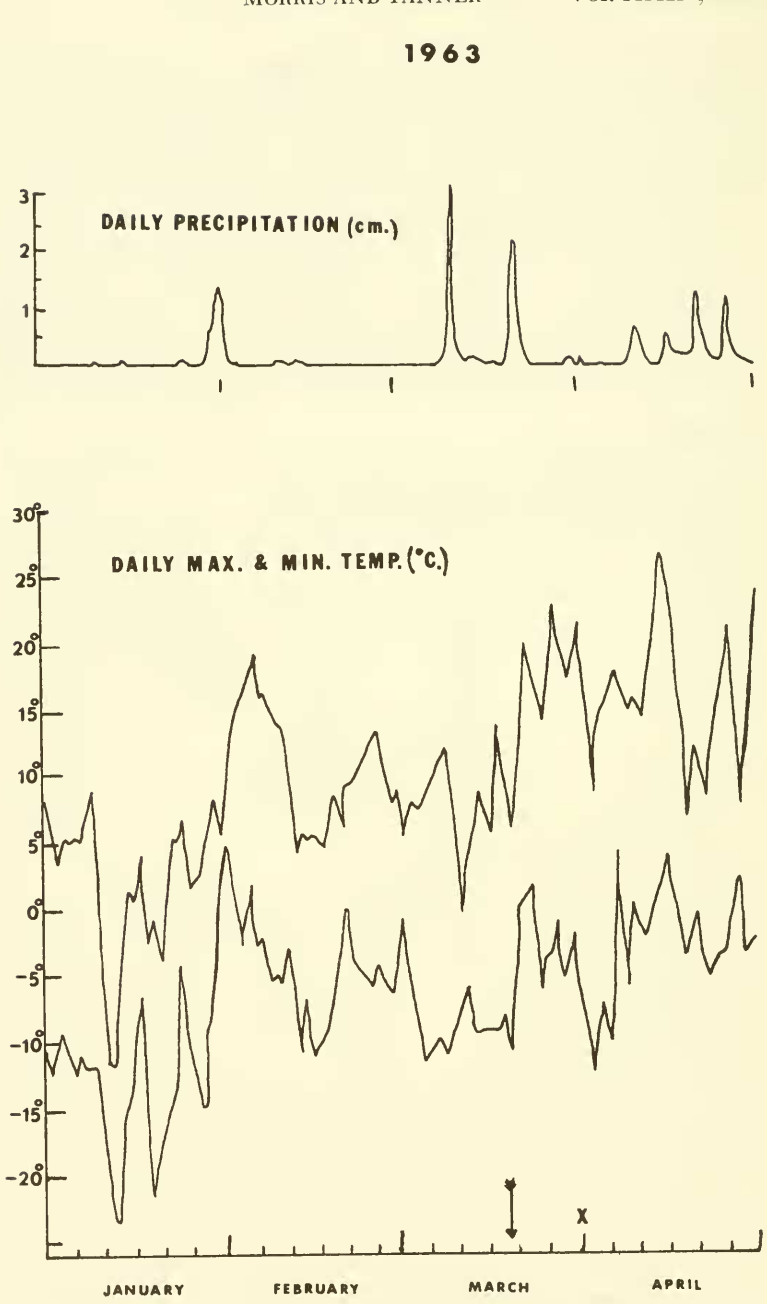

Fig. 6. Climatic data for the spring of 1963. Arrow indicates approximate date of emergence; X indicates approximate date hatching began.

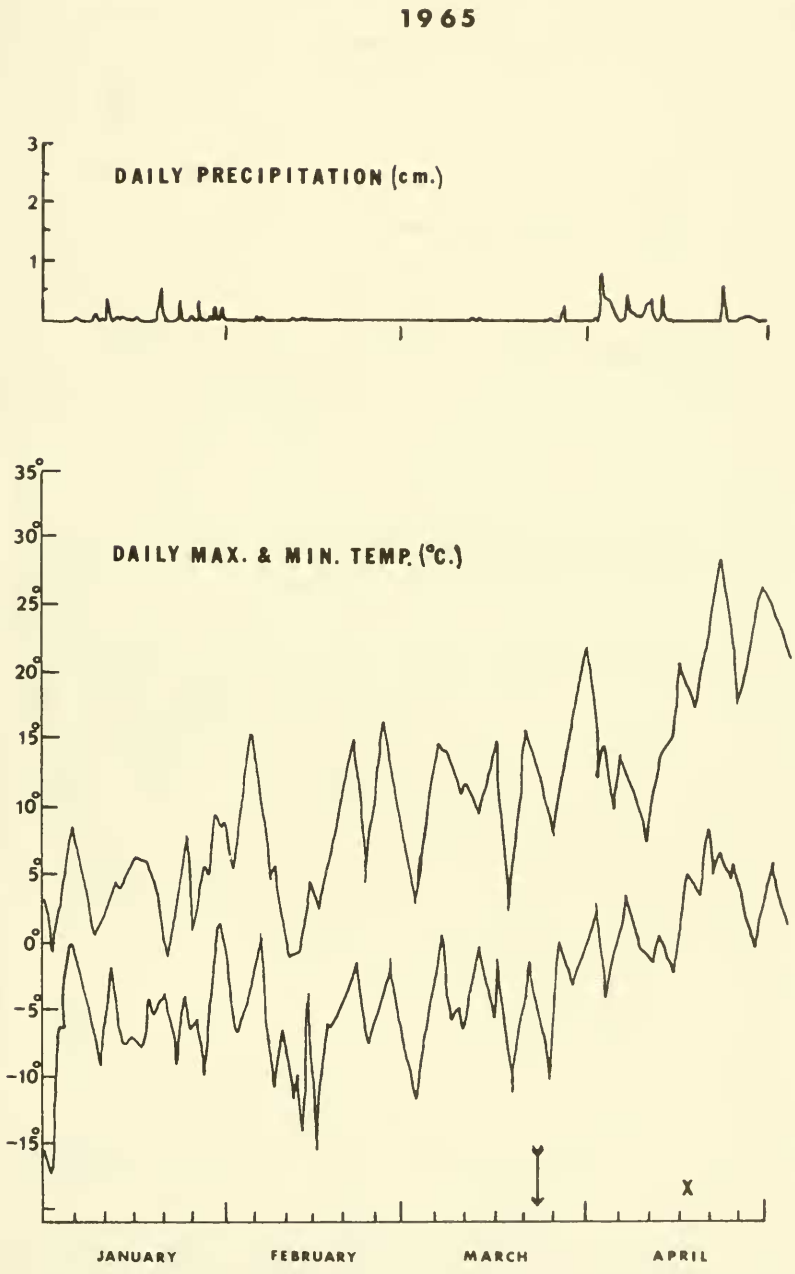

Fig. 7. Climatic data for the spring of 1965. Arrow indicates approximate date of emergence; X indicates approximate date hatching began.

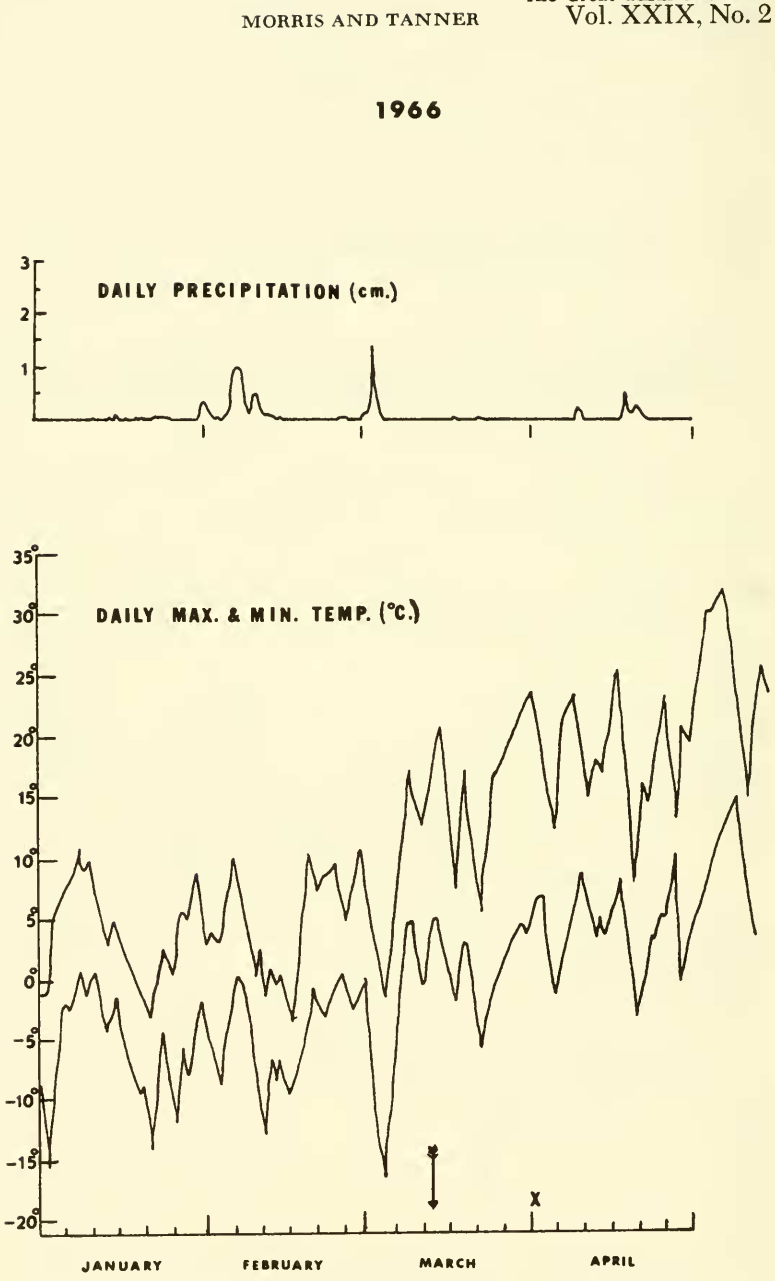

Fig. 8. Climatic data for the spring of 1966. Arrow indicates approximate date of emergence; X indicates approximate date hatching began.

ture to release them from hibernation, but when early morning temperatures fall below 10° C, or during a cold period causing a similar drop, frogs are not found at the surface of the water. Dredging of the bottom of the ponds reveals their presence in a semidormant state. As the temperature of the water again warms to 10° C they can be seen resting in vegetation just under the surface of the water. As the temperature warms to 11° C they will come to the surface.

There are undoubtedly other factors involved in stimulating their release from hibernation. The effect of moisture has been mentioned by both Vernberg (1953) and Martof (1953) as being important in releasing amphibians from hibernation.

During the spring of 1966 and 1967 it was noticed at two separate locations that frogs were appearing later in those ponds where the water level had dropped so that in the more shallow portions of the ponds the bottom was exposed. There may have been several factors involved in their retarded arrival, two of which may have been a lower temperature or a greater fluctuation in temperature because of a smaller quantity of water. This is an area of study open to further investigation. However, one item was noted, namely that these receding ponds showed a greater concentration of soluble salts, approximately 100 ppm higher than the others. This may possibly provide a type of physiological dryness to the frogs causing a delay in their appearance.

The males are first to appear and are present three or four days before the larger females emerge. The smaller immature frogs do not appear for two or three weeks after the females or until the breeding season is completed.

A summary of measurements taken on 36 frogs collected and released at study area II, pond A, on March 27, 1966, can be found in Table 2.

Table 2. Measurements of postbreeding frogs taken March 27, 1966, from study area II, pond A.

Sex	Number of specimens	Snout-vent length in mm	
		Range	Mean
Female	5	78.6-61.6	70.0
Male	25	64.2-47.2	49.9
Immature	6	42.6-31.0	37.8

As males emerge they do not exhibit much activity and can be found either calling from the pond with only their heads above water, or buried in vegetation during a cold period.

Vocality. The call itself closely resembles the sound made by repeatedly clicking the tongue against the top of one's mouth. The calls come in a series of clicks ranging in number from six to approximately 50. The rate of the notes varies depending upon the temperature. An examination of several calls made at 16° C showed a var-

iance in rate of from 300 notes per minute to 480 notes per minute by different males. The duration of an individual call is from 4-10 seconds and repeated at a rate of as many as 10 calls per minute. With each note the floor of the mouth is depressed approximately 2 or 3 mm. The call can be given either above or below the surface of the water with the call from below the surface being somewhat louder. The call is weak and is muffled when other anuran species are calling from the same pond. The maximum distance for hearing the call is somewhat less than 25 meters, the average being 7 to 10 meters. The call of one male has been observed to stimulate others to call. This was noted after the frogs had been disturbed and many moved to the bottom of the pond. As one came near the surface and called, other frogs came from under the vegetation and swam to the top as if responding to a signal; soon all were at the surface and calling again. Normally at this time they pay little attention to any movement around the pond, even to the point that many can actually be touched before they attempt to escape.

Mating. Mating takes place immediately upon the arrival of the female as evidenced by the following: (1) at no time was an adult female observed to be present which was not in amplexus until after ovulation, and (2) the aggressiveness with which males attempt amplexus would require only a few minutes before a receptive gravid female would be clasped. The sexual drive is very strong in males of this species, so much so that not only do they attempt amplexus with others of the same sex, but at times two and three males have been observed embracing one female (Fig. 9); however, this multiple

Fig. 9. Multiple embrace of two males with one female. Note typical position of calling males at breeding sites.

embrace lasts for only a few minutes. The drive is so strong that attempted amplexus has been observed with other objects in the water, even to the point that one male, rather than escaping as it was reached for, swam closer and clasped onto my finger. The tenacity to mate is no doubt correlated with competition exerted by the large male to female ratio, and the fact that this species is very gregarious with all of the breeding activity limited to a small area within the pond. Of 30 adult frogs collected on March 27, 1966, there was a 1 to 5 female to male ratio (Table 2).

The difference in size between the larger females and smaller males (Table 2) places the vent of the males directly above that of the females during amplexus. Amplexus is axillary with the male embracing from above.

Ovulation. The females are apparently ready for ovulation as soon as they emerge and several clutches of eggs have been observed the same day. The eggs are normally laid at a water temperature of approximately 14° C and may be laid during the day or night. In nature, egg-laying has been observed to be interrupted for several days during a cold period, but would proceed as soon as the water again warmed to the approximate temperature. The embrace is maintained during the entire period. Experimentally males have maintained the clasp in the laboratory during a lowering of temperature almost to the point of freezing at which time the clasp was slowly released. Throughout the entire period of amplexus, the male's main physical activity seems to be to maintain the clasp until ovulation. All activities, such as protection and movement into deeper water during cold periods, are dependent upon the action of the female. The male remains passive during the entire period.

Fertile eggs have not been taken from a clasping pair which have been removed to the laboratory. This artificial condition seems to inhibit the females from laying even though the males have maintained their embrace for as long as two weeks.

The actual process of ovulation has not been observed in nature, although eggs have been found before the first cleavage has taken place. An examination of a clutch of eggs collected March 29, 1966, at study area III, showed that some eggs were attached together by a small gelatinous chord 2 to 3 mm in diameter as reported by Turner (1958), whereas the surfaces of adjacent eggs were attached directly by 3 to 5 mm of their outer membrane. A close examination of a typical egg revealed that it was connected to five other eggs. Two of these adjacent eggs were attached by means of the gelatinous chord, while the other three were attached directly by their outer membranes. As eggs are laid the adhesive character of the membranes causes them to become attached to one another and form one large, irregular clump. They also weakly adhere to vegetation below them as they come in contact with it.

Oviposition sites. The sites used for egg laying have several characteristics in common: (1) they are normally in the part of the

pond which has warmest temperature resulting from solar radiation, and in most instances this is on the west side where the eggs catch the morning sun; (2) the eggs were always laid in an open area in clear water and never in among the cattails or in floating *Spirogyra* which was oftentimes only a few feet way; (3) eggs are usually in the shallow portion of the pond 10 to 20 cm under the surface of the water and attached to *Chara sp.* This attachment is rather weak, however, and within a week the clutch usually breaks loose and floats on the surface where the eggs become more of a flattened mass and are scattered by wind and water movements.

As one clutch of eggs is laid, there apparently is a stimulation for other females to lay their eggs in the same area. This behavior was best shown at study area IV where approximately 50 clutches of eggs were laid within an area 75 cm in diameter, even though other apparently ideal locations were available. This large assemblage of eggs was weakly attached, one to another and to the vegetation (Fig. 10). In this large pond area only a few clutches were found away from the large mass of eggs.

Eggs. During the spring of 1965, 10 clutches of eggs were measured and counted in the field (Table 3). The average number of eggs per clutch was 605. The largest clutch contained 725 eggs and the smallest 430 eggs.

In 1966 eggs in 21 different clutches were counted and measured (Table 4), and the average number per clutch for this year was 746. The maximum was 1160 and minimum 147 eggs per clutch.

Fig. 10. Oviposition site at study area IV. Note the closeness of egg masses (approximately 50 clutches).

Table 3. Comparison of clutch size and number of eggs collected from study area I on March 30, 1965.

Total no. Eggs per clutch	Clutch size in cm	Diameter of eggs in mm	
		Egg	Outer Mem.
541	9-8-5	2.5	10.0
625	9-7-5	2.3	10.1
695	11-8-7	2.4	10.5
715	10-8-7	2.5	13.0
615	12-9-9	2.5	10.0
635	11-9-7	2.4	10.0
650	13-9-7	2.5	13.0
725	11-6-6	2.2	10.7
514	6-5-3	2.1	12.0
430	5-4-2	2.3	11.0

Table 4. Relationship of clutch volume and number of eggs per clutch.

Locality	Date	Total no. eggs per clutch	Clutch volume in cc	Eggs per cc of clutch
Study area II pond A	24 March 66	940	320	2.62
		660	110	6.00
		500	105	5.24
		900	215	4.37
		950	400	2.38
	29 March 66	600	400	1.50
		840	415	2.02
Stury areaII pond B	29 March 66	716	285	2.58
		900	475	1.72
		148	130	1.13
		1160	550	1.11
	30 March 66	980	500	1.96
	31 March 66	655	325	2.01
		625		
Study area III	23 March 66	900	285	3.17
		925	230	3.96
		380	115	3.30
		460	100	4.60
Study area IV	5 April 66	990	250	3.96
		716	235	3.05
		730	375	1.98

Because of the great variation in egg numbers and because the numbers were consistently lower than those reported by such workers as Svihla (1935). Livezey and Wright (1947), Wright and Wright (1949), and Stebbins (1951), it was suspected that perhaps these frogs were laying a small number of eggs at one location and then producing others later, as was reported by Bragg (1944) for the common leopard frog in Oklahoma. However, in the dissection of gravid females of *R. p. pretiosa* from Utah County, this same variation in numbers has been observed before any eggs had been laid (Table 5). Therefore, it is reasonable to assume that Utah populations produce a smaller number of eggs for each complete clutch.

Table 5. Comparison of egg numbers and size of females collected from study area II, pond A.

Date	Total no. eggs per clutch	Clutch volume in cc	Eggs per cc of clutch	Total length of female
27 July 66	902	80	11.3	74
19 August 66	763	50	15.2	73
13 September 16	168			67
7 October 66	860	60	14.4	70
8 October 66	1060	72	14.7	64
15 October 66	393	40	11.2	59

We are unable to explain the reason for variation in the number of eggs per clutch. The size of females does not reliably explain the variation in clutch size.

Freshly deposited eggs soon increase in volume by absorption of water, so that within several hours after laying they may range from 110 cc to 550 cc with the average of those measured being 291 cc. Clutches of the same age are variable as to size and number of eggs per cc as is indicated in Table 3.

Several days after being deposited, a clutch usually appears as an irregular, oval mass just under the surface of the water. Within about a week egg mass becomes less coherent, and breaks loose to float at the surface in more of a plinth shape. By the time the eggs are ready to hatch they are almost undiscernible from above, because of the accumulation of dirt and debris on the exposed surface and the breaking up and amalgamation of the adjoining jelly masses. There is also a dry, crusty appearance to the mass resulting from destruction of 10 to 20 percent of surface eggs. This high mortality rate among the eggs is a result of several factors. First, the eggs are laid early in the spring so that there are many nights in which they become encrusted in ice which destroys some of them. Also, because of the long period of embryonic development they may later be forced out of the water by the new growth of submerged vegetation, which exposes the top eggs to desiccation.

Each egg is enclosed in two gelatinous envelopes separated by an indistinct inner membrane. The total diameter of the outer capsule normally varies within a range of from 9.0 mm to 13.0 mm although variations as great as 8.0 mm to 21.0 mm have been measured. The average diameter of those eggs measured (Tables 3, 6-9) was 10.0 mm. The diameter of the indistinct inner membrane has a normal variation of from 3.8 mm to 6.1 mm and a mean of 5.0 mm. This membrane is difficult to see in the fresh eggs without the techniques employed as described previously, but can be seen even in unfertilized eggs if these methods are used. As development progresses this inner membrane becomes more obvious because of the infestation of algae from the outside which stops at the inner membrane. If eggs fail to develop the ovum deteriorates clouding the inner jelly coat out as far as the inner membrane.

Table 6. Measurements in mm of eggs collected March 29, 1965, at study area I.

Egg Diameter	Capsule Diameter	
	Inner	Outer
2.7	5.0	10.0
2.8	6.0	13.0
2.7	4.9	12.0
2.6	5.0	10.0
2.0	4.7	11.0
2.5	4.9	11.0
2.4	3.8	11.0
2.1	4.5	10.0
3.0*	8.0*	21.0*

*Extremely large egg

Table 7. Measurements in mm of unfertilized eggs laid in the laboratory by a female collected March 27, 1967, at study area III.

Egg Diameter	Capsule Diameter	
	Inner	Outer
2.5	4.7	9.0
2.4	4.7	9.0
2.6	4.9	8.0
2.7	4.8	10.0
3.0	5.0	11.0
2.8	5.0	12.0
2.8	5.0	12.0

Table 8. Measurements in mm of eggs collected March 29, 1966, at study area III.

Egg Diameter	Capsule Diameter	
	Inner	Outer
2.6	6.0	11.0
2.5	6.1	10.1
2.4	5.2	10.0
2.4	5.0	8.0

Table 9. Measurements in mm of eggs collected April 5, 1966, at study area IV.

Egg Diameter	Capsule Diameter	
	Inner	Outer
2.6	5.0	10.6
2.6	5.0	10.5
2.6	3.0	10.0
2.7	5.1	10.3
2.6	5.0	10.3
2.5	4.5	10.2
2.4	4.9	10.1

The ovum is normally 2.5 mm in diameter, but does vary within a range of 2.1 to 2.9 mm. Preservation can cause some distortion in size if not done properly and may account for some of the variation shown in Tables 3, 6-9. The color of an egg is dark brown to black above, and pale yellow or light tan below. The vitelline membrane is closely applied to the ovum at time of hatching, which allows an enlargement of the fluid-filled chamber for embryonic development and movements.

As the embryonic development progresses, the embryo becomes progressively longer until at the time of hatching it is 8 to 10 mm in length. An attempt to analyze the physical factors involved in the actual hatching process has not been made. Discussions of these factors are given by Noble (1954) and Bragg (1940a, 1940b). A change in temperature was observed to have a noticeable influence on the hatching process. This was demonstrated when eggs placed in a natural spring did not hatch even though embryonic development seemed to be complete. The temperature of the spring water remained constant, at approximately 11° C, with only minor fluctuations. Samples of these eggs when removed from the cold environment would hatch in approximately one hour while those left in the spring hatched 7-10 days later. Eggs which were brought into the laboratory hatched at room temperature in about seven days, whereas those in nature and subject to the lower temperatures required from 13 to 23 days to hatch. Under normal pond temperature where the eggs were laid, the majority hatched about two weeks after ovulation. However, length of time required for hatching varies from year to year depending upon the fluctuations of atmospheric temperatures and the amount of cloud cover which reduces solar radiation.

Larval Period. The hatching activities cover a period of several days, with most eggs hatching within three weeks after ovulation. The tadpoles remain attached to the gelatinous material by their oral suckers for two or three days following hatching. As they break loose from the jelly they sink to the bottom where only an occasional swimming movement is made. The results of ciliary movement along the body surface keeps a fresh supply of oxygenated water flowing from anterior to posterior past their external gills, as observed under a dissection microscope (30x mag.). The mouth and anal openings do not develop until one or two days following hatching. Actual feeding begins in conjunction with the first swimming activities. Associated with this free feeding stage, an operculum develops over the external gills and water is taken in through the mouth and out the spiracle on the left side of the body. The food eaten is mostly secured by scraping or rasping off the loose outer surface of decomposed plant material, a function for which the teeth are well adapted.

The rows of larval teeth are two upper and three lower as described by Skousen (1952) except that in a high percentage of the specimens measured, the first lower row was continuous rather than divided medially. For a more complete discussion on the development of larval mouth parts see Johnson (1965). An examination of the

digestive tracts of several larvae show mostly decomposed material and some green algae. Tadpoles in the laboratory have been raised on live *Spirogyra* which gives a green color to the digestive tract. Burke (1933) was able to raise *Rana pretiosa* tadpoles through metamorphosis on a 24 hour mixed culture of bacteria. He concluded that the common water bacteria contain all the food factors necessary for their normal growth. The scavenger feeding of tadpoles advanced beyond stage 26 (Table 10) was further observed as they ate the remains of dead *pretiosa* tadpoles.

Table 10. Summary of developmental stages.

Stage 1:	Egg fertilization
Stage 2:	Appearance of the Gray Crescent
Stage 3:	Two cells (first cleavage)
Stage 4:	Four cells
Stage 5:	Eight cells
Stage 6:	16 cells
Stage 7:	32 cells
Stage 8:	Mid cleavage
Stage 9:	Late cleavage
Stage 10:	Beginning of gastrulation
Stage 11:	Involution at dorsal lip
Stage 12:	Blastopore complete
Stage 13:	Neural plate develop
Stage 14:	Neural folds and groove formed
Stage 15:	Beginning of ciliary rotation, closing of neural fold
Stage 16:	Neural tube formed, gill plates discernible
Stage 17:	Development of tail bud
Stage 18:	Muscular movement
Stage 19:	Heart beat
Stage 20:	Gill circulation
Stage 21:	Cornea becomes transparent, mouth opens
Stage 22:	Tail fin circulation
Stage 23:	Opercular fold formed
Stage 24:	Operculum covers right gills
Stage 25:	Operculum covers left gills
Stage 26:	Hind limb bud appears
Stage 27:	Limb bud length equal to or greater than one-half the diameter
Stage 28:	Limb bud length equal to or greater than diameter
Stage 29:	Limb bud length equal to or greater than one and one-half the diameter
Stage 30:	Limb bud length equal to two times the diameter
Stage 31:	"Foot" becomes paddle shaped
Stage 32:	Indentation formed for fourth and fifth toes
Stage 33:	Indentation formed between third and fourth toes
Stage 34:	Indentation formed between second and third toes
Stage 35:	Indentation formed between first and second toes
Stage 36:	Beginning of toe separation
Stage 37:	All toes separated
Stage 38:	Appearance of metatarsal tubercles
Stage 39:	Subarticular tubercles appear as light patches on the inner surface of the foot
Stage 40:	Subarticular tubercles fully developed
Stage 41:	Loss of cloacal tail piece, "skin window" appears for forelimb
Stage 42:	Forelimbs free
Stage 43:	Angle of mouth midway between nostril and eye
Stage 44:	Angle of mouth below midpoint of eye
Stage 45:	Angle of mouth posterior to eye, tail stub remains
Stage 46:	Metamorphosis complete

The actual growth of tadpoles, like that of the unhatched embryos is greatly influenced by different temperatures (King, 1903; Moore, 1938; Brattastrom, 1963; and Johnson, 1965). Tadpole activities at the early stages indicate that they employ to some extent a biological control of their temperature by their position within the pond. The young tadpoles prefer to stay close to the bottom and do so in the shallower areas where water temperature during the day is warmer. Aggregations of tadpoles have been noted at various times throughout the summer and as suggested by Carpenter (1953b) and Brattstrom (1962) these close aggregation may contribute, because of their melanistic color, to the warming of their immediate surroundings by absorption of solar radiation which in effect speeds up development leading towards metamorphosis. On overcast and rainy days tadpoles move to deeper water and are usually within the vegetation. By stage 30 (Table 10) they become more active, continually swimming and feeding throughout the pond. This activity continues until metamorphosis at which time a modification of the digestive tract permits them to feed closer to the shore on small arthropods, and to rest in the vegetation.

Summary of Developmental Stages. To facilitate a description of the developmental process taking place in embryonic (prefeeding stage) and larval (free feeding stage) frogs, staging tables have been used. They are of value in a life history study since the external morphology of each stage of development is described and illustrated. These staging tables have been used for some time by authors in descriptive and taxonomic works. Two systems of numbering the stages were in use until Gosner (1960) presented a table which simplified them. Johnson (1965) described and illustrated the stages as they applied to the spotted frog, *Rana pretiosa luteiventris*.

Table 10 is a summarization from Gosner (1960) and Johnson (1965), and is used as a standard of comparison since growth rates are too variable from one locality to another to be used for this purpose.

Growth Rate. The embryonic growth up through stage 27 (transformation stage from embryo to larvae) is dependent upon food stored in the yolk. All growth beyond this stage is dependent upon the tadpole's own feeding. For this reason no constant measurements of growth were taken until this stage. Those tadpoles which developed at warmer temepratures reached this stage in a shorter period of time and were 2 to 3 mm longer in total length. Study site II, pond B, continually maintained a 4-8 C warmer temperature than pond A until the middle of September when they became equivalent. An average of temperature readings taken at different hours of the day throughout the larval period shows pond A with 13.6 C and pond B with 18.7° C. The more rapid development resulting from the warmer temperature at pond B was, however, counteracted by the crowded conditions imposed upon the tadpoles when a screen, (Fig. 2) was placed around some of the eggs. The effects of the screen were evident by the middle of May when it was obvious that the growth

of the tadpoles at pond A exceeded that of the now stunted tadpoles of pond B (Fig. 11). Another factor which may have had an effect upon the growth of the tadpoles at pond B was the high concentration of dissolved salt in the water. The concentration was 622ppm at pond B as compared with a 380 ppm reading at pond A. Pond B also had a pH of 8.9 compared with a 7.7 at pond A. A detailed study of dissolved minerals was not made; however, their effects prove to be very similar to those causing the stunted condition in plants grown in the same concentration of minerals because of the checked absorption of water.

Cameron (1940), in a summary of his work, stated that for *Rana pipiens*:

> 1. The nature and amount of dissolved substances and their relative proportions exert separate and unlike influences upon the rate of development and the stage attained at hatching of normal frog embryos. Eggs kept in well water containing fluorine hatch earlier but at a less advanced stage of development than those kept in pond or distilled water.
>
> 2. Flourine in concentrations as low as 1 ppm is able to exert a constant and measurable retardation on the rate of development and stage at hatching.

The tadpoles of pond B showed their greatest rate of growth from April 10 to May 23. At the end of this time their total length varied within a range of from 33 to 47 mm (Fig. 11). This growth rate was a maximum of approximately 2.7 mm per day and a minimum of 1.5 mm per day since stage 26. The development stage at the end of this growth period varied from 33 to 37 (Fig. 12) indicating that the greatest period of growth was from the first appearance of the hind limb bud until the full development of the hind foot. There was no appreciable growth from May 23 to July 27. The ontogenetic development, however, had advanced to a stage where several of the larger tadpoles were transforming into frogs (Fig. 12). This transformation of larger tadpoles seemed to release some of the growth retarding effects on smaller ones (Fig. 16-21). Thus, there followed another period of increased growth so that by the end of August their total length varied from 40 to 57 mm. Rose (1960) stated that when stunted tadpoles were separated from their larger siblings normal growth again took place.

The tadpoles of pond A continued their growth until stage 40 when metamorphosis began without any noticeable decrease in the growth rate (Fig. 13); therefore, tadpoles at this pond had mostly transformed into immature frogs by the end of August. Although the development of larvae at Pond A was approximately two weeks later than at pond B, they developed at the same rate until the first of June at which time the tadpoles of pond B became stunted (Fig. 12.)

The individual size of each tadpole showed signs of variability shortly before the hatching stage and these differences became more exaggerated with their development. Cameron (1940) suggested that

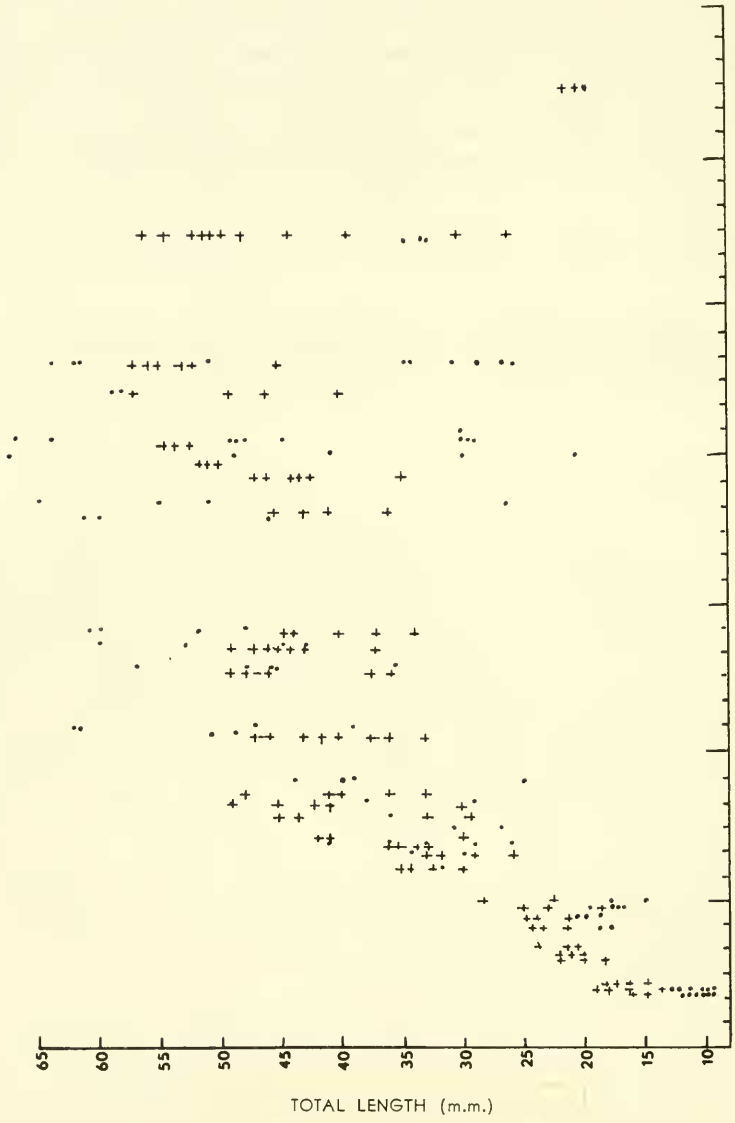

Fig. 11. Scatter diagram showing total length of specimens collected randomly at study area II on days indicated. Dots are pond A and crosses are pond B.

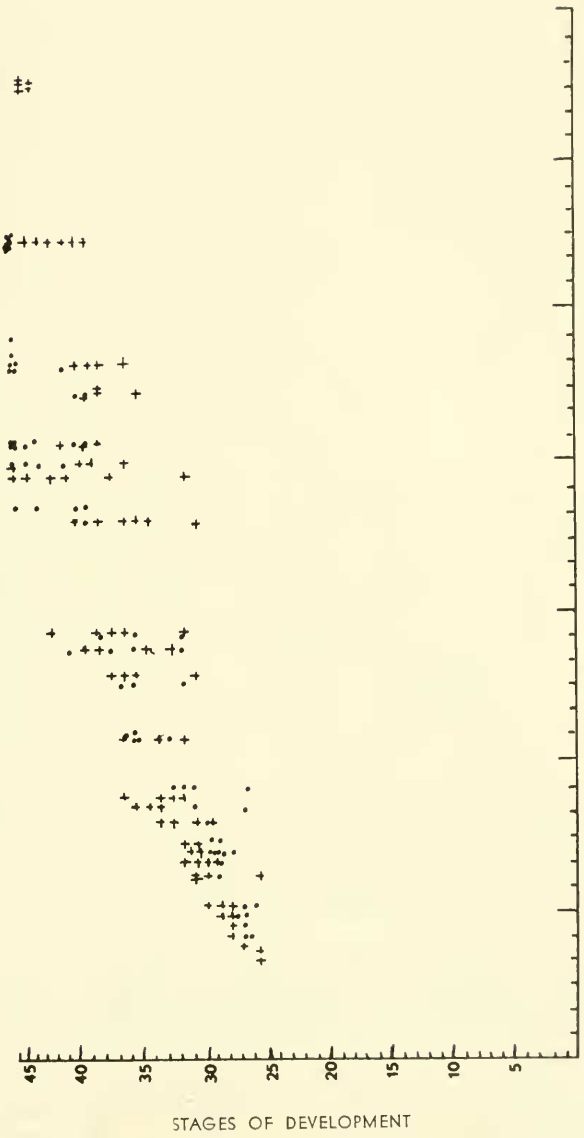

Fig. 12. Scatter diagram showing stages of development of specimens collected randomly at study area II on days indicated. Dots are pond A and crosses pond B.

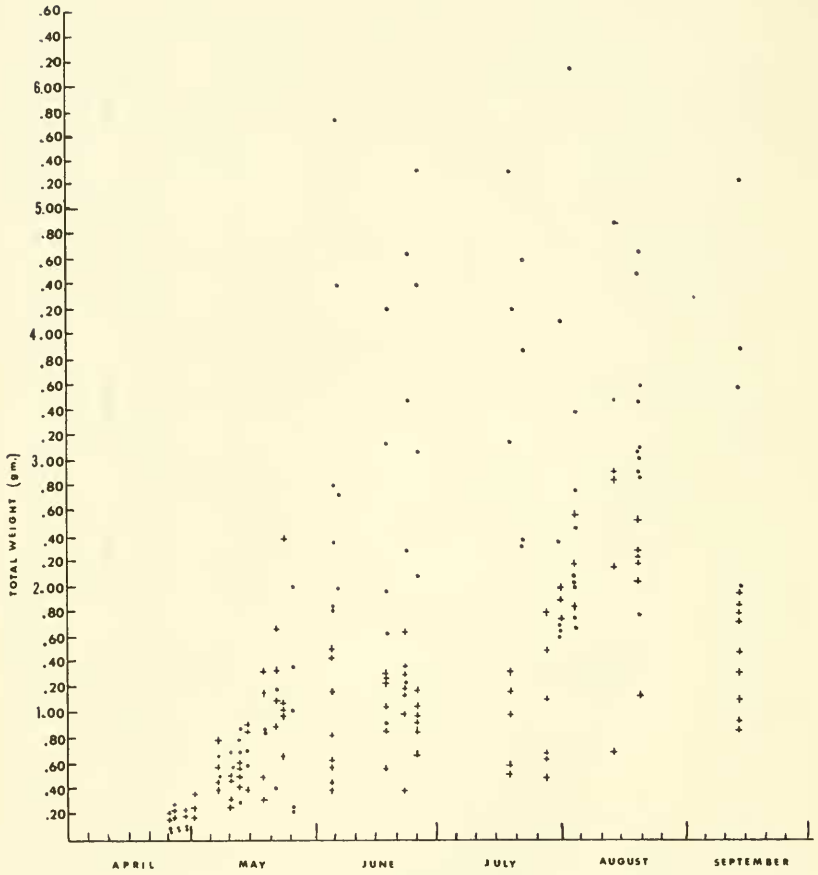

Fig. 13. Scatter diagram showing total weight of specimens collected randomly at study area II on days indicated. Dots are pond A and crosses pond B.

there is a genetic variation of as much as 10 percent in the size of eggs reaching a given stage. This difference in size was more apparent at pond A where the total mass of the individuals, as shown by the weights in Fig. 11, on August 3, had a range of 1.69 to 6.12 gm.

An examination of Figs. 11-13 shows that absolute body dimensions are so variable throughout the larval development that the use of these measurements as key characters in species identification would be most difficult. The use of body ratios as suggested by Limbaugh and Volpe (1957) is also questionable since there is a variance from one individual to another even in those of the same age (Fig. 14). Data show that the larger tadpoles have a smaller tail to head ratio, and when the head length is greater than 24 mm the tail can have a variance of approximately 23 mm (21 to 44 mm) (Fig. 16).

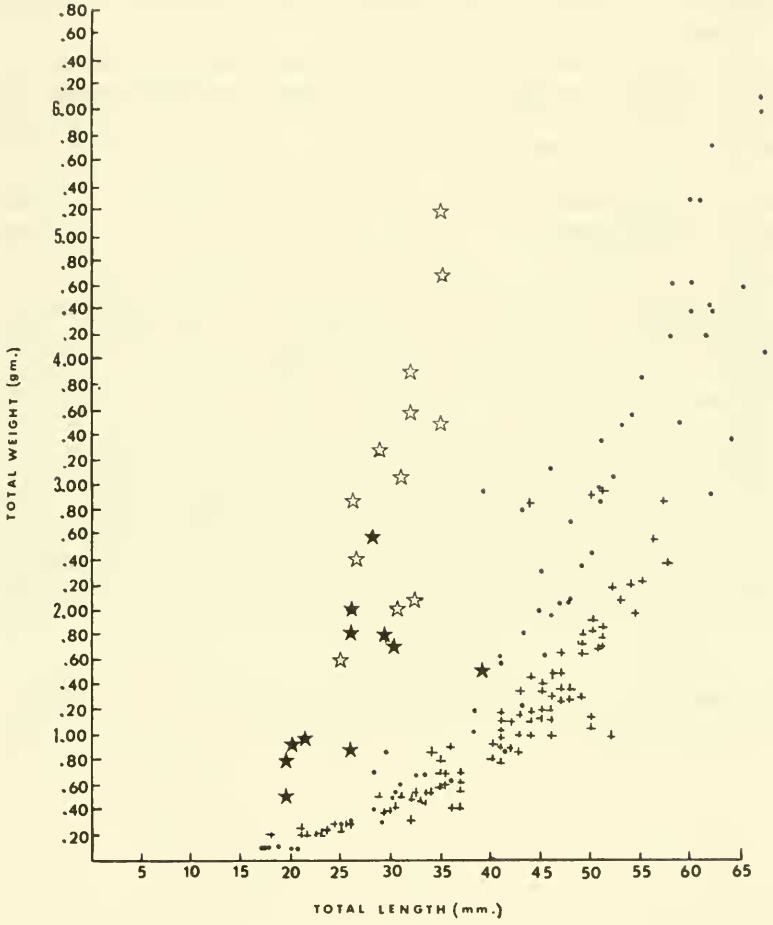

Fig. 14. Scatter diagram showing comparison of length and weights of specimens collected randomly at study area II. Dots indicate specimens up through stage 45 at pond A, crosses indicate specimens up through stage 45 at pond B, open stars indicate specimens past stage 45 at pond A, and closed stars indicate specimens past stage 45 at pond B.

Tadpoles at pond A normally began metamorphosis, stage 41, once they reached a maximum total length of 50-55 mm (Fig. 11, 12 and 15). Some tadpoles, however, continue to grow even after others of approximately equal size have begun transformation, so that they reached a maximum size of up to 70 mm two or three weeks later. There is a tendency for these large tadpoles to remain in an arrested state of development between stages 36 and 40 once they have grown past the normal size for transformation. They remained as large tadpoles up until the last of August before any started to transform

and then all were able to complete metamorphosis by September 15, 1966.

The tadpoles at pond B were not only retarded in size (as a group), but also retarded in their ontological development (Fig. 12 and 15). The first transformation was on August 3, 1966, two weeks later than the first tadpoles from pond A (Fig. 12). Transformation was a slow process, requiring until October 15, 1966, for the remainder of the population to complete metamorphosis (Fig. 12). Therefore, the time required for metamorphosis to occur at this locality varied from 122 days to a maximum of 209 days after egg laying.

The maximum and minimum total lengths of tadpoles at pond B reaching stage 40, were 57 to 47 mm respectively (Fig. 15), compared with the same maximum and minimum of 70 and 60 mm at pond A. An examination of Fig. 14 gives another picture of the smallness of transforming frogs from pond B. When comparing their weights with total length, the pond B tadpoles are consistently smaller at the time of metamorphosis, with the smallest weighing 0.52 gm and a total length (snout-vent) of 19.5 mm. This would indicate that in some tadpoles very little growth would have taken place since the middle of May (when the stunted condition developed) because they were approximately the same head-body (snout-vent) length and total weight as the tadpoles on May 23 (Fig. 13). It soon

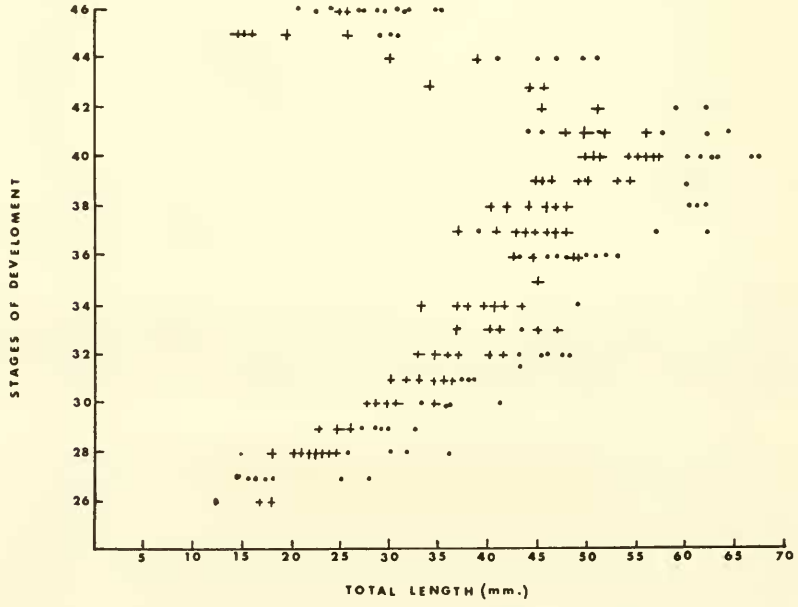

Fig. 15. Scatter diagram showing comparison of total length and stage of development of specimens collected at study area II. Dots indicate pond A and crosses pond B.

becomes apparent that size is not one of the stimulating factors in metamorphosis (Fig. 14), but rather metamorphosis is dependent on an internal reaction.

Once metamorphosis begins (stage 41) the time required to complete the transformation (stage 46) is comparatively short. A series of 10 tadpoles at stage 40 were examined to determine the time required for the appearance of the front legs. The front leg is the first to appear and the joint of the elbow can be seen appearing out of the spircular opening for 3 to 4 hours before the full leg becomes apparent. Only an occasional three legged frog will be observed in nature because of the brevity of this stage. Of the 10 specimens examined after the left leg appeared, the time varied from 4 to 8 hours before the right leg appeared. Detailed descriptions of the tadpoles are given by Stebbins (1951), Skousen (1952), Turner (1958), and Johnson (1965), and it is for this reason that we have not included detailed descriptions.

Hibernation. The ponds at study area II were checked at inervals during the fall of 1966 to determine the data of disappearance for hibernation. Both frogs and tadpoles were seen until the first of October, but by the 15th all of the tadpoles had metamorphosed and were basking at the edge of the pond. The adult frogs were seen in the deeper water among the cattails. The next observation was October 27 at five o'clock p.m. The water temperature at this time was 9° C at pond A and 14° C at pond B; no frogs were evident. The air temperature had been down to freezing for several nights since the last visit, but it had taken about two weeks for the water to cool to or below the critical 10° C level (Fig. 16). The frogs had been observed in about the same location of the pond throughout the sum-

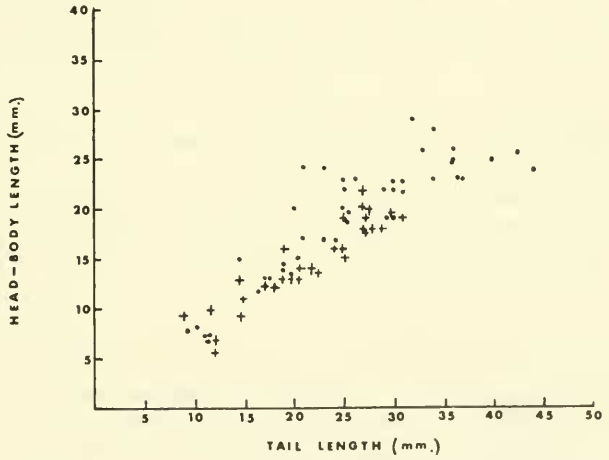

Fig. 16. Scatter diagram showing comparison of tail and head-body lengths up through stage 40 of specimens collected at study area II. Dots are pond A and crosses pond B.

mer and right up until the time of hibernation. It is assumed, therefore, that these frogs hibernate in the muck under the same water in which they breed.

Conclusions and Summary

This study was in progress with some interruptions from 1962 to 1967 for the purpose of investigating the breeding biology and life history of *Rana pretiosa pretiosa* Baird and Girard in central Utah. Some effects of various environmental factors upon the growth and habits of this species were considered.

Collections were made from the time the adults emerged from hibernation in the spring until the tadpoles metamorphosed and frogs hibernated in the fall. Data gathered at the ponds and samples of the life history stages were taken to the laboratory where they were analyzed and studied.

The western spotted frogs emerged from hibernation normally during the middle of March as a result of the warming of the environment. This same species does not emerge until May at Yellowstone National Park, Wyoming (Turner 1958), but is usually present by late February in Washington (Svihla 1935). A few individuals were reported by Dickerson (1906) to be out sunning themselves throughout the winter at Puget Sound.

In Utah this species prefers small ponds of standing water grown thick with stonewart and possessing a deep muck bottom from which cattails emerge. Tanner (1931) in speaking of the Utah population states, "it is always found near springs, small streams, and swamps." Turner (1958) recorded them as visitors of "pools of stagnant water . . . " for egg deposition. Stebbins (1966), however, reported the habitat as follows: "A highly aquatic species found in the vicinity of cold, permanent water—streams, rivers, marshes, springs, pools, and small lakes. Seems not to occur in warm stagnant ponds grown to cattails."

The adult male frogs appear in large numbers at the beginning of the breeding season, which begins immediately following the emergence of the larger females. The emergent male frogs seem to congregate in small areas of the ponds as breeding choruses. The breeding season usually lasts for a short period and all eggs are laid within a week or two depending on prevailing temperatures. The males outnumber the females by a ratio of 5 to 1, thus there is strong competition for a mate. The strong sexual drive in the males may be the result of this strong competition.

The voice of the male is characterized by a low clicking sound which can be reproduced by clicking ones tongue against the top of his mouth. The call is very weak and can normally be heard for only 20-30 feet. The distance compares favorably with that reported by Turner (1958), but is considerably less than the quarter of a mile reported by Svihla (1935). Stebbins (1966) stated that the call was unknown in *Rana pretiosa*.

The eggs are laid shortly after the arrival of females and vary in number from 147 to 1160 per clutch, the average being approximately 750 per clutch. The range of eggs per clutch is lower than the 1100 to 1500 reported by Svihla (1935). It is, however, higher than the 206 to 802 reported by Turner (1958). Turner (1958) reported that his eggs numbers were based upon counts of eggs in clusters 1 to 3 days old; Svihla's (1935) reported that the number is an estimation based upon two egg masses which measured 1500 cc and 1100 cc. His determinations were made as follows: "Since each egg measured more than 1 cc the number of eggs in these masses would approximate 1500 and 1100 respectively." Because these same 1100 and 1500 figures are reported by Livezey and Wright (1947), Wright and Wright (1949), and Stebbins (1951), and on the basis of data gathered for this study, it appears that no actual counts were made by these authors and that their numbers are, at least for the Utah population, too high.

The eggs average 2.5 mm in diameter and are surrounded by a distinct outer gelatinous envelope and an indistinct inner one, averaging 10.0 and 5.0 mm respectively. Following the key prepared by Livezey and Wright (1947), these populations are *R. p. pretiosa*.

The eggs have required from one week to hatch in the laboratory to 13-23 days in nature, the majority hatching about two weeks after oviposition. This two week incubation period is the same as that required by the frogs in Wyoming as reported by Turner (1958), but longer than the four days given by Carl (1943) for those in British Columbia. Johnson (1965) reported the eggs as taking 72 hours to hatch at 25° C but longer at cooler temperatures.

Several factors were noted which affect the frogs' growth and behavior. These were temperature, crowding, and perhaps dissolved minerals in the water.

Temperature has an effect upon all stages of the life history of the frog. The adult activity seems to be affected by temperatures approximately 10-11° C. Temperatures below this point bring on a quiescence in their activities. The eggs are laid at temperatures above 14° C. These temperatures are higher than the 5° C which Middendorf (1957) reported as being critical in the frogs' activity. The eggs and tadpoles are subject to a wide range of temperature but growth is more rapid at the warmer temperatures. Johnson (1965) found 6° and 28° C to be the minimum and maximum temperatures limiting normal embryonic development for this species. Other studies on temperature tolerance and rates of development are by Moore (1938, 1939, and 1942).

A high concentration of soluable salts in the water was suspected of having retarding effects both upon the spring emergence of the adults and the growth of the larvae. Cameron (1940) observed that low concentrations of flourine retarded development. Gosner and Black (1957) studied the effects of acidity on the development and hatching of frogs, while Merwin and Allee (1943) noted the retarding effects of carbon dioxide on the cleavage rates of frog eggs.

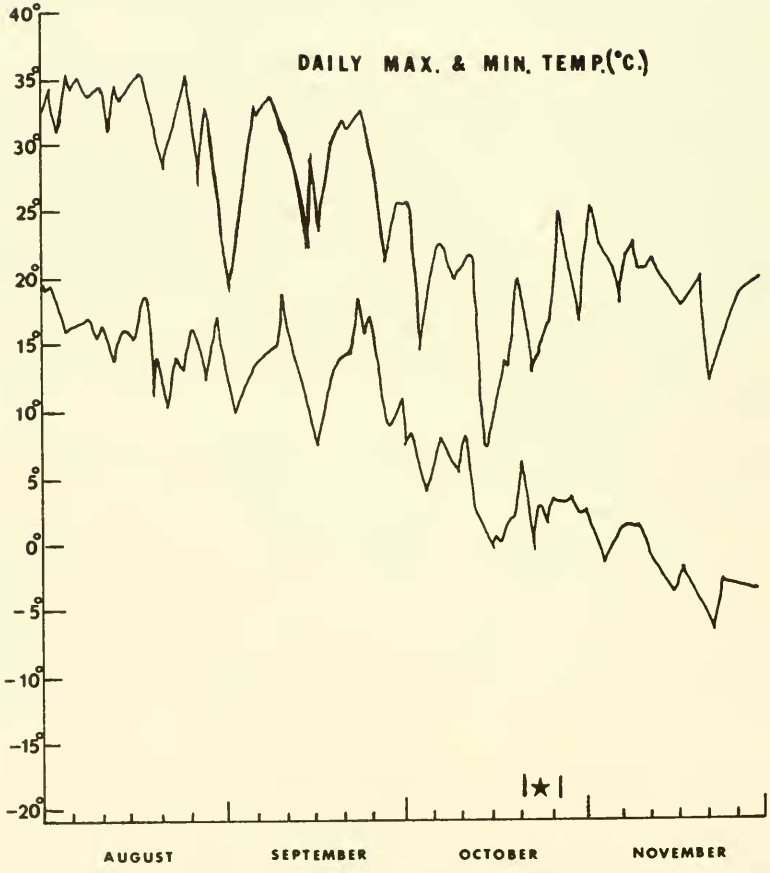

Fig. 17. Air temperature for the fall of 1966. Stars indicate approximate date of hibernation.

Crowding of tadpoles was observed to have a retarding effect upon size and development. This same phenomonon has been observed and studied by Lynn and Edelman (1936), Rose (1960), Adolph (1929), Rugh (1934), and Richards (1958) in other species of Anura.

Metamorphosis was observed to begin on July 27, 1966; this was approximately 122 days following ovulation. Some tadpoles required up to 209 days to transform. It may therefore be concluded that at higher elevations or more northern latitudes having a shorter summer that tadpoles may require more than one summer to complete their growth and to transform as reported by Logier (1932) in British Columbia and Turner (1958) in Wyoming.

An examination of the larval mouth parts reveals a tooth row formula of two rows and three lower rows which according to Svihla (1935) would place them as *R. p. luteiventris*.

Hibernation began during the middle of October approximately two weeks after the first freezing temperatures, and presumably under the same water where their summer atcivities were concentrated.

The adults are variable in key characteristics and normally are classified as *R. p. pretiosa*. The ventral coloration is variable between orange and red. The following color description given by Stebbins (1966) does not fit the Utah population: "Populations in Nevada, Utah, Idaho south of Salmon River, and SE Oregon usually have yellowish ventral color; elsewhere red or salmon predominates."

The Utah *pretiosa* do not completely fit present keys to the subspecies and have been identified in various studies as either *pretiosa* or *luteiventris*. The taxonomic characters examined in this study show an intergradation of sub-specific types. Based upon the eggs and adult coloration we consider the Utah population to be *Rana p. pretiosa*. The susceptibility of the larvae to different water conditions may be the factor which limits the distribution of the subspecies rather than the differences in the adults which seem to be ecologically similar. Wright and Wright (1949) in giving the distribution of the *pretiosa* subspecies state that *luteiventris* occupies the tertiary volcanic areas, whereas *pretiosa* prefer the continental deposit areas. The key to the taxonomy and distribution of this species may very well be the differences in ecological tolerance of the immature frog rather than the adults.

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